New species of grammitid ferns (Polypodiaceae, Polypodiopsida) from Bolivia

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Abstract

We describe 14 new species from the genera \textit{Ceradenia}, \textit{Grammitis} s.str., and \textit{Lellingeria}, and provide keys to the Bolivian species of \textit{Ceradenia} and \textit{Lellingeria}.

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Introduction

Grammitid ferns are a group of about 750 species characterized by green, usually tetrahedral spores, sporangial stalks of only one row of cells, scaleless leaves, and almost always by leaf traces of single vascular strands (Parris 1990, 1998; Ranker et al. 2004). They have been treated as a distinct family (e.g. Newman 1840; Ching 1940; Parris 1990; Ranker et al. 2004) or as part of the family Polypodiaceae (e.g. Tryon and Tryon 1982; Lellinger 1989; Smith et al. 2006). Molecular studies have shown that the grammitids are a monophyletic lineage nested within Polypodiaceae (Ranker et al. 2004; Schneider et al. 2004). Generic delimitation within grammitid ferns is highly controversial, with only one genus recognized by Tryon and Tryon (1982); Lellinger 1989; Smith et al. 2006). Molecular studies have shown that the grammitids are a monophyletic lineage nested within Polypodiaceae (Ranker et al. 2004; Schneider et al. 2004). Generic delimitation within grammitid ferns is highly controversial, with only one genus recognized by Tryon and Tryon (1982), 4 genera by Parris (1990), 10 by Smith (1993), 12 by Copeland (1956), and 18 by Parris (2003). The difficulty in dividing grammitid ferns into genera is due to the high variability and homoplasy of obvious morphological traits such as blade dissection, and the rather obscure nature of taxonomically informative traits such as hydathodes, rhizome symmetry, root insertion, or even presence of fungal bodies on the blades (Smith 1993; Ranker et al. 2004). Based on these and other characteristics, Bishop (1988, 1989), Smith et al. (1991), Bishop and Smith (1992), Smith (1992, 1993), and Smith and Moran (1992) defined 10 genera among the neotropical representatives of the grammitid ferns, with another genus described since then (Murillo and Smith 2003). A recent molecular review of the grammitids by Ranker et al. (2004) has shown that these genera mostly correspond to monophyletic lineages, but that some genera are polyphyletic or paraphyletic.

During our studies of Bolivian ferns, we have encountered numerous undescribed species of grammitid ferns. We here describe 14 new species from the genera \textit{Ceradenia}, \textit{Grammitis} s.str., and \textit{Lellingeria}, and provide keys to the Bolivian species of \textit{Ceradenia} and \textit{Lellingeria}. We do not include \textit{Melpomene} and the species groups of \textit{Terpsichore lanigera} and \textit{Terpsichore alsopteris}, because these are currently the subject of monographic studies. In accordance with Bishop (1988),
we define *Grammitis* to contain only species with simple blades and dark, sclerotic laminar margins. Keys to the genera of neotropical grammidids are provided by Smith (1993) and Moran and Riba (1995).

There are 96 species of grammidid ferns known from Bolivia. While some are common and widespread within the country, it is striking how many species are known from one or a few collections and/or localities. Many species appear to be very rare, and have been collected only once even in well-studied localities visited repeatedly by several botanists. It is expected that additional collecting activity will reveal additional species for the Bolivian flora.

The large number of previously undescribed species, especially in *Ceradenia*, might surprise those unfamiliar with Andean grammidids. There are several reasons for the high number of new taxa. Most genera have never been monographed, and many species are small and inconspicuous, or superficially resemble one another. Even more importantly, as discussed above, many species appear to be naturally rare and/or local. While the population ecology of grammidids remains unknown, it may be hypothesized that small, localized populations favor genetic divergence of populations and hence speciation. Further, as a result of their rarity and inconspicuous nature, many species are poorly collected, especially in Bolivia, which is one of the botanically least known countries in Latin America.

Taxonomic section

*Ceradenia ayopayana* M. Kessler & A.R. Sm., spec. nov.

(Fig. 1A–C)

Etymology

Named for the province Ayopaya in Cochabamba department, which harbors a rich and unique fern flora, including several locally endemic and undescribed species, and the only known South American population of *Polystichum turrialbae* H. Christ (Fjeldså et al. 1999; Smith et al. 1999).

Type

Bolivia, Depto. Cochabamba, Prov. Ayopaya, San Cristobal, subiendo por el sendero que va a San Miguel, 16°39′S, 66°43′W, 3100 m, 6 June 2002, Jimenez 1114. Holotype: LPB; isotypes: GOET, UC.

Diagnosis and description

Inter species *Ceradenia* subgeneris *Filicipecten* notabilis petiolis gracilibus, foliis textura tenue, longe linearibus, pinnatisectis, pinnis brevibus latisque, petioli et pinnis setis pallide brunneis, 1–1.5 mm longis obitis.

Plants epiphytic; rhizomes slender, short-creeping to erect, with orange-brown scales 0.8–1.5 × 0.3–0.4 mm, with hyaline marginal setulae; petioles pale brown, 30–80 × 0.2–0.3 mm, with 2–3-celled glandular hairs 0.1–0.3 mm and scattered pale brown setae to 1.5 mm, about as long as the lamina, slightly flexed distally; rachis sclerenchyma on both sides of blades not exposed, with moderately dense pale brown setae to 1.5 mm abaxially; laminae erect to arching or pendent, linear, abruptly reduced at base or with one to four slightly reduced proximal pinna pairs, apices subabruptly reduced, sometimes with a distinct apical segment, percurrent throughout with up to 40 pinna pairs, to 16 cm long; pinnae to 20 × 5 mm, almost entire to repand, inserted about 60° to the rachises, at base constricted acroscopically and decurrent basiscopically, apices rounded to apiculate, with pale brown setae to 1.5 mm long along margins and laminar surfaces abaxially, costal sclerenchyma exposed, veins mostly simple, a few one-forked, texture thin-herbaceous; sori medial to supramedial, to four pairs per pinna, superficial, lacking setae but sporangia mixed with numerous, stalked, gland-tipped paraphyses.

Distribution and ecology

Endemic to Bolivia. At the type locality on the west slope of the Cordillera Cocapata, *Ceradenia ayopayana* was found as a locally uncommon epiphyte in disturbed evergreen cloud forests at 3100 m (I. Jimenez pers. comm.), while the paratypes consist of only two collections of a single plant each found in an intensively studied primary cloud forest at 3000 and 3300 m. Most forest cover in this region has been destroyed by agricultural activities; only scattered forest patches remain (Fjeldså et al. 1999). Further, climatic conditions change over very short distances on the Cordillera Cocapata, and suitable forest habitats are likely to be naturally locally distributed. As a result, *C. ayopayana* may be threatened.

Remarks

This new species belongs to subg. *Filicipecten*, which is characterized by dorsiventral and solenostelic rhizomes, absence of wax-like laminar glands, and petiolate laminae (Bishop 1988). In this subgenus, *C. ayopayana* is unique by its slender petioles and long-linear, thin-herbaceous leaves with short, broad pinnae. It is most similar to *Ceradenia madidiensis*, from which it differs by shorter and relatively broader, more strongly ascending pinnae, paler setae, and thinner petioles.

Additional specimens examined

Bolivia. Depto. La Paz, Prov. Nor Yungas, Estación Biológica de Tunquini, senda nueva del camino de la
mina (curva al lado oeste) al pantánón, 16°11'S 67°53'W, 3000 m, 14 September 2000, Bach 1050 (LPB); same locality, 3300 m, 19 September 2000, Bach 1096 (LPB).

Ceradenia clavipila L.E. Bishop ex M. Kessler & A.R. Sm., spec. nov.  
(Fig. 2A–C)

Etymology
The late L.E. Bishop first recognized this species as undescribed in 1988, and coined the name.

Type

Diagnosis and description
Differt a speciebus similibus subg. Filicipectenis setis marginalibus pinnarum castaneis et setis paginae pin-narum et venarum destitutis.

Plants epiphytic; rhizomes stout, with dark orange-brown to dark castaneous rhizome scales 5–8/0.2–0.4 mm, these with paler marginal setulae; petioles atropurpureous, to 320/1.2 mm, glabrous or with a few scattered castaneous setae to 1.5 mm proximally, about as long as, or much longer than, the laminae; rachises abaxially with sclerenchyma exposed on proximal half, dark brown to greenish, glabrous or covered with abundant pale castaneous setae to 1 mm, adaxially with sclerenchyma exposed for almost the entire length, dark
brown, with numerous pale castaneous setae to 1.2 mm; laminae lanceolate, to 33 cm long, usually broadest just above the base (lowermost one to two pinna pairs somewhat reduced), apices gradually reduced without a distinct apical segment, pinnatisect, basally sometimes fully pinnate, pinnae to 70 × 6 mm, entire or moderately crenate, inserted 70–85° to rachises, at base sometimes constricted acroscopically and de-current basiscopically, apices acuminate, surfaces glabrous or with a few, scattered setae on the costae, margins with few to numerous dark castaneous setae to 1 mm, texture thick-chartaceous; sori supramedial, to 19 pairs per pinna, superficial, lacking setae, sporangia mixed with numerous, stalked, gland-tipped paraphyses.

**Distribution and ecology**
Central Peru and Bolivia. A locally fairly common epiphytic species in humid montane forests at 2750–3400 m.

**Remarks**
This species is characterized by the castaneous rhizome scales 5–8 × 0.2–0.4 mm, castaneous, marginal setae on the pinnae, and by lacking setae on the pinna surfaces and veins. The holotype and Bach 1048 have glabrous lower rachises, whereas the other specimens cited bear setae in various degrees of density. There is also variation in the color of the rhizome scales, ranging from dark orange-brown to dark brown. As both the density of setae on the rachises and the scale color appear to change clinally and are not correlated with
each other, we consider all studied specimens to belong to a single, variable species. More collections and detailed field studies are needed to better understand the variation of this species or species complex.

Additional specimens examined

**Ceradenia glabra** M. Kessler & A.R. Sm., spec. nov. (Fig. 2E–G)

**Etymology**
The name alludes to the essentially glabrous blades.

**Type**

**Diagnosis and description**
Species unica in subg. *Filicipecten* rhachide ubique dense setosa et pinnis subglabris (pilis minutis margina-libus exceptis) notata.

Plants epiphytic; rhizomes stout, with orange-brown rhizome scales to 10 × 0.6 mm, these with pale marginal setulae; pelti adaxially scissuripurpureous, shining, to 300 × 2 mm, glabrous, about as long as the lamina; rachises axially with sclerenchyma exposed only proximally, dark brown to greenish, with numerous castaneous setae to 0.5 mm, adaxially with sclerenchyma exposed for almost the entire length, dark brown, with abundant castaneous setae to 1 mm; laminae lanceolate, broadest just above the base (lowermost one to two pinna pairs somewhat reduced), pinnatisect to basally fully pinnate, to 25+ cm long, apices gradually reduced, pinnatisect; pinnae to 90 × 6 mm, entire or slightly repand, inserted 75–90° to rachises, at base usually constricted acroskopically (especially on the proximal pinnae) and decurrent basiscopically, apices acuminate, surfaces glabrous, margins glabrous or with scattered pale, 2–4-celled, sometimes forked marginal hairs to 0.1 mm, texture thick-chartaceous; sori supramedial, to 28 pairs per pinna, superficial, lacking setae, sporangia mixed with numerous, stalked, gland-tipped paraphyses.

**Distribution and ecology**
Ecuador and Bolivia. In Ecuador, it is locally common at 2400–2600 m in stunted ridge forest dominated by *Puridiae nutans* (Clethraceae). In Bolivia, *Ceradenia glabra* is known only from two collections made at 2700 m in humid montane forests in one of the most intensively botanically studied areas of the Bolivia Andes, and thus appears to be genuinely rare.

**Remarks**
This large *Ceradenia*, which belongs to subg. *Filicipecten*, is similar to *C. kookenanae* (Jennem) L.E. Bishop and *C. kalbreyeri* (Baker) L.E. Bishop in having the pinna margins without setae but with small, pale, simple or forked hairs. *C. glabra* differs from these species by having large, orange-brown rhizome scales, abundant
Ceradenia jimenezii M. Kessler & A.R. Sm., spec. nov.

(Fig. 1D–F)

Etymology

We name this species after the Bolivian botanist I. Jimenez, whose keen eyes have detected a surprising number of new species of grammitids in the last few years.

Type

Bolivia, Depto. La Paz, Prov. Nor Yungas, Cerro Hornuni, por el sendero nuevo que va a la 3ra estación climatológica, 16°12'S, 67°53'W, 3070 m, 24 October 2000, Jimenez 371. Holotype: UC, isotype: LPB.

Diagnosis and description

Differs from Ceradenia capillare (Desv.) L.E. Bishop petiolis tenuioribus setibus destitutis, squamis rhizomatis longioribus et pinnis latioribus distincte distantibus. Plants epiphytic; rhizomes slender, erect, with orange-brown scales 1.5–3 × 0.2–0.4 mm bearing scattered marginal glands; petioles brown, 5–20 × 0.2–0.3 mm, with whitish to pale brown, 2–5-celled glandular hairs 0.15 mm, about 0.1 times the length of the laminae, not flexed distally; rachises with sclerenchyma exposed on both sides, with whitish to pale brown, 1–3-celled glandular hairs 0.1 mm on both laminar sides and along the margins, costal sclerenchyma exposed; texture thin-herbaceous; sori inframedial, to four pairs per pinna, superficial, lacking setae but sporangia mixed with numerous, stalked, gland-tipped paraphyses.

Distribution and ecology

Endemic to Bolivia. Ceradenia jimenezii is a fairly common epiphyte in wet cloud forests at the type locality on Cerro Hornuni in Cotapata National Park (I. Jimenez pers. comm.). Surprisingly, it has not yet been found along the well-collected sites around Unduavi, Coscapa, Cotapata, and Chuspipata, only 10–15 km to the south, indicating that it may be very local. The type locality is protected in the national park and under no immediate threat.

Remarks

This species belongs in subg. Ceradenia, characterized by radially symmetric and dictyostelic rhizomes, wax-like glandular laminar hairs, and short-petiolate or sessile laminae (Bishop 1988). It is most similar to Ceradenia capillaris (Desv.) L.E. Bishop, from the Antilles to Colombia, Venezuela, Guyana, Ecuador, Peru, and southern Brazil, but differs by its thinner petioles lacking setae, longer rhizome scales, and well-spaced, broader pinnae. The only other species in the group of C. capillaris that also lacks setae on the petioles and rachises is Ceradenia mirabilis L.E. Bishop, which has bipinnate fronds and filiform rhizome scales (Bishop 1989).

Additional specimens examined

Same locality as holotype, 3100 m, 19 December 2000, Jimenez 33 (LPB), Jimenez 42 (GOET, LPB, UC); Prov. Nor Yungas, Estación Biológica de Tunquini, senda al oeste del pantánón, 16°12'S 67°54'W, 3000 m, 13 July 2002, Bach 1841 (LPB, UC); Prov. F. Tamayo, PN-ANMI Madidi, senda Pelechuco-Mojos, localidad Tambo Quemado (lugar para acampar), entrando por la ladera E de la quebrada en que se unen los dos rios abajo de Tambo Quemado, 14°41'S 68°58'W, 3360 m, 5 March 2003, Jimenez 1844 (LPB, UC).

Ceradenia kalawayae M. Kessler & A.R. Sm., spec. nov.

(Fig. 1G–H)

Etymology

Named after the Kalaway healers of the Charazani region, who use over 1000 plant species in traditional medicine; but whether the present species is also used is unknown.
Type

Diagnosis and description
Species in subg. Ceradenia notabilis characteribus sequentibus: squamae rhizomitae parvae marginibus glandulosus, lamina profunde pinnatifida, laminae, rhachides et petiolo copiouse glandulis pallidis regulariter ordinatis obseitae, lamina setis destituta.

Plants saxicolous or epiphytic; rhizomes slender, erect, with orange-brown to reddish brown scales 1–1.8 × 0.2–0.3 mm with 2–3-celled, gland-tipped marginal hairs; petioles dark brown, 8–35 × 0.4–0.6 mm, with whitish to pale brown, 2–6-celled, partly 2–5-branched glandular hairs to 0.15 mm, about 0.1–0.5 times the length of the lamina, not flexed distally; rachises with sclerenchyma exposed abaxially, with abundant, whitish to pale brown, 2–5-celled, partly 2–4-branched glandular hairs to 0.15 mm; laminae erect, lanceolate to linear, to 16 cm long, narrowed at the base with two to three gradually reduced pinna pairs, pinnatisect, with about 10–40 pinna pairs, apices gradually reduced; pinnae to 13 × 4 mm, closely spaced to separated by about their width, inserted 50–55° to rachises, sinuate, slightly widened at base, especially basiscopically, apices rounded to acuminate, laminae with numerous, regularly spaced, whitish to pale brown, 2–3-celled glandular hairs 0.15 mm on both laminar sides and along the margins, costal sclerenchyma exposed abaxially; veins in some specimens ending in hydathodes adaxially; texture thin-herbaceous; sori medial to inframedial, to five pairs per pinna, superficial, lacking setae but sporangia mixed with numerous, stalked, gland-tipped paraphyses.

Distribution and ecology
Endemic to Bolivia. Ceradenia kalawayae is an uncommon saxicolous species, collected at 3100–3400 m in humid cloud forests with Weinmannia, Clusia, and Chusquea.

Remarks
The generic affinities of this distinctive species are uncertain. The waxy glands on the petioles, laminae, and sori suggest a placement in Ceradenia, but the hydathodes and small rhizome scales with glandular margins are very unusual in that genus. The only other known hydathodous species in Ceradenia is the recently described Ceradenia tryonorum (León and Smith 2003), which, however, differs in having elongate sori, long petioles, thick and spongy laminae, and larger rhizome scales; the two species may not be closely related. Until the relationships among Andean grammitids are better understood, it seems best to place C. kalawayae in Ceradenia subg. Ceradenia where it cannot be confused with any other known species due to its hydathodes, small rhizome scales with glandular margins, deeply pinnatifid leaves (vs. fully pinnate leaves in most other species), and the absence of setae.

Additional specimens examined
Bolivia, Depto. La Paz, Prov. Nor Yungas, Cerro Hornuni, por el sendero nuevo que va a la 3ª estación climatológica, 16°12’S, 67°53’W, 3100 m, 19 December 2000, Jimenez 37 (LPB); Prov. F. Tamayo, PN-ANMI Madidi, senda Pelechuco-Mojos, Tambo Quemado, antes de llegar al 3° rio, abajo de Tambo Quemado, 14°41’S 68°58’W, 3410 m, 5 May 2003, Jimenez 1862 (LPB, UC).

Ceradenia madidiensis M. Kessler & A.R. Sm., spec. nov.
(Fig. II–K)

Etymology
Named for the Madidi National Park in northwestern Bolivia, one of the most species-rich protected areas worldwide (Jørgensen et al. 2005).

Type
Bolivia, Depto. La Paz, Prov. Franz Tamayo, PN-ANMI Madidi, senda Keara–Mojos, Tambo Quemado, lugar para acampar, 14°41’S, 68°58’W, 3570 m, 29 April 2003, Jimenez 1801. Holotype: UC, isotype: LPB.

Diagnosis and description
Species nova Ceradeniae subgeneris Filicipectinis characteribus sequentibus notabilis: folia pinnatisecta vel pinnatisecta-pinnatifida, pinnae basi parum constrictae, setae castaneae, 1–1.8 mm longae in petiolis, rhachidibus et pinnis, textura foliorum tenuis.

Plants epiphytic; rhizomes slender, erect to suberect, with red-brown scales 1–1.5 × 0.3–0.4 mm, with hyaline marginal setulae; petioles brown, 20–35 × 0.3–0.5 mm, proximally glabrous, distally with a few scattered castaneous setae to 1 mm, 0.25–0.7 times the length of the laminae, not flexed distally; rachises abaxially; veins in some specimens ending in hydathodes adaxially; texture thin-herbaceous; sori medial to inframedial, to five pairs per pinna, superficial, lacking setae but sporangia mixed with numerous, stalked, gland-tipped paraphyses.
castaneous setae to 1.8 mm long along margins and costae abaxially, a few scattered setae on the laminae, costal sclerenchyma exposed; texture thin-herbaceous; sori medial, to five pairs per pinna, superficial, lacking setae but sporangia mixed with numerous, stalked, gland-tipped paraphyses.

**Distribution and ecology**

Endemic to Bolivia. At the type locality, *C. madidiensis* was a locally fairly common epiphyte in disturbed evergreen timberline cloud forests at 3600 m with *Polylepis sericea* (Rosaceae) as the dominant tree species (I. Jimenez pers. comm.). Among the paratypes, Kessler 11748b consists of a single plant collected in disturbed, *Weinmannia*-dominated cloud forest at 3450 m. At this site, which is easily accessible and has been a favorite haunt of fern collectors since the times of Otto Buchten in the 1910s, the species is evidently rare. As this species is apparently restricted to timberline habitats and *Polylepis* forests on the humid eastern Andean slope in La Paz department, Bolivia, it could be gravely threatened by the extensive burning of timberline habitats that has taken place for thousands of years and that has lowered the upper timberline by 500–800 m (Kessler 2000).

**Remarks**

This new species belongs to subg. *Filicipecten*. It most closely resembles *Ceradenia semiadnata* (Hook.) L.E. Bishop, a little-known species from the Ecuadorian and Colombian Andes, from which it differs in the paler abaxial, squamae rhizomatis atrocastaneae, margine et in superficie setulis provisae, pinnae latae sub angulo 80–90° a rachidi patentes. Plants epiphytic; rhizomes stout, with dark castaneous scales to 5 × 0.5 mm, these with hyaline setulae along the margins and on the scale surfaces, especially towards the scale base; petioles dark brown, to 170 × 1 mm, with scattered pale castaneous setae to 2 mm, 1–2.5 times as long as the lamina; rachis sclerenchyma adaxially exposed, dark brown, abaxially covered by green tissue, both sides with abundant castaneous setae 0.3–0.5 mm; laminae triangular, with proximal pinna pair usually the largest, apices gradually reduced without a distinct apical segment, pinnatisect, to 10 cm long; pinnae to 40 × 4 mm, entire, inserted 80–90° to rachises, basiscopically widened and decurrent at base, acroscopically slightly adnate, apices narrowly rounded, with numerous dark castaneous 0.3–0.5 mm setae on the abaxial lamina surfaces and costae, these often abraded leaving dark scars, margins with regularly spaced reddish setae to 1 mm, adaxially with numerous reddish setae to 1 mm, texture thick-chartaceous; sori supramedial, to 15 pairs per pinna, superficial, lacking setae, sporangia mixed with numerous, stalked, gland-tipped paraphyses.

**Distribution and ecology**

Endemic to Bolivia. Known only from the type collection made in humid cloud forest at 2900 m.

**Etymology**

The name refers to the setae on the rhizome scales.

**Type**

Bolivia, Depto. Cochabamba, Prov. José Carrasco Torrico, 8 km de Empalme hacia Siberia, 17°46'S, 64°48'W, 2900 m, 22 October 1996, Kessler 9204. Holotype: GOET; isotypes: LPB, UC.

**Diagnosis and description**

Species nova *Ceradenia* subg. *Filicipecten* characteribus sequentibus: laminae setis abundis in pagina abaxiali, squamae rhizomatis atrocastaneae, margine et in superficie setulis provisae, pinnae latae sub angulo 80–90° a rachidi patentes.

**Additional specimens examined**

Bolivia, Depto. La Paz, Prov. Franz Tamayo, PN-ANMI Madidi, senda Karea-Mojos, Tambo Queiado, lugar para acampar, 14°41'S, 68°58'W, 3600 m, 15 November 2001, Jimenez 1089 (LPB, UC); Prov. Nor Yungas, Trocha al Valle de Coscapa, P.N. Cotapata, 16°12'S, 67°53'W, 3450 m, 9 September 1997, Kessler 11748b (LPB, UC).

*Ceradenia pilipalaea* M. Kessler & A.R. Sm., spec. nov. (Fig. 2N–P)

**Remarks**

This is another species with abundant, regularly spaced setae abaxially on the pinnae and is therefore closely related to *Ceradenia pilipalaea* and *Ceradenia similis*. It is, however, distinct in bearing setae on the rhizome scale surfaces, and (in Bolivia) in having slightly
adnate acrosopic pinna bases. It shares the adnate pinna bases and dark rhizome scales with *Ceradenia tristis* from Costa Rica, but that species lacks setae on the rhizome scale surfaces and has glabrous laminar surfaces.

*Ceradenia pilipecten* L.E. Bishop ex M. Kessler & A.R. Sm., spec. nov.

(Fig. 2K–M)

**Etymology**
This species was already recognized and provisionally named, but never described, in the late 1980s by the late L.E. Bishop.

**Type**
Bolivia, Depto. Cochabamba, Prov. Ayopaya, Comunidad Pampa Grande, antes de llegar al primer rio que atravieza la senda desde Tunki, 16°40′S 66°28′W, 2030 m, 09 November 2002, Jimenez 1533. Holotype: UC; isotypes: GOET, LPB.

**Diagnosis and description**
Species nova *Ceradeniae* subg. *Filicipecten* characteribus sequentibus: laminae setis abundis in pagina abaxiali, squamae rhizomatis aurantiaco-brunneae, margine setulis 0.5–1 plo quam latitudo squamae, pinnae latae sub angulo 80–90° a rhachidi patentes.

Plants epiphytic or epipetric; rhizomes stout, with brown rhizome scales with marginal setulae 0.5–1 times as long as the scale width; petioles dark brown to atropurpureous, to 170 mm long, with proximal pinna pair usually the longest, apices gradually reduced with a sometimes slightly prolonged apical segment, pinnatisept, proximally sometimes fully pinnate; pinnae to 40 × 4 mm, entire, inserted 80–90° to rachises, widened and decurrent at base, especially basiscopically, apices narrowly rounded to acute, with numerous dark castaneous setae 0.3–1.5 mm on the abaxial lamina surfaces and costae, margins with regularly spaced dark brown setae to 1 mm, adaxially with fewer scattered setae on the costae, texture thick-chartaceous; sori supra- medial, to 18 pairs per pinna, superficial, lacking setae, sporangia mixed with numerous, stalked, gland-tipped paraphyses.

**Distribution and ecology**
Peru and Bolivia. Fairly common, epiphytic and saxicolous species in humid submontane and montane forests between 990 and 2490 m.

**Remarks**
*Ceradenia pilipecten* belongs to a problematic species complex with *Ceradenia spixiana* (Mart. ex Mett.) L.E. Bishop, *C. tristis* A.R. Sm., *C. similis*, and *C. pilipalaea*. Among these, *C. pilipecten* is characterized by abundant castaneous setae on the abaxial pinna surfaces, orange-brown rhizome scales with marginal setulae 0.5–1 times as long as the scale width, and broad pinnae inserted 80–90° to rachises. It may be confused with *C. spixiana*, which has more flaccid, longer (to 7 mm), bright golden-brown rhizome scales with longer setulae, and usually has only a few setae shorter than the marginal ones on the abaxial laminar surfaces. However, some young leaves of *C. spixiana* from Bolivia (e.g. Krömer & Acebey 807, GOET) have quite dense, long hairs adaxially on the laminae. Clearly, the species limits in this group are ill-defined and call for either very broad species delimitations or several narrowly defined species. We choose the latter course, because the extreme forms of this complex (*C. spixiana* and *C. pilipalaea*) are so dissimilar that few taxonomists would accept their placement in a single species, even though they are joined by a range of apparently intermediate forms. Bishop (1989, p. 14) pointed out that the subg. *Filicipecten*, to which these species belong, “seems analogous in complexity and similarity to the *Poy podium vulgare* complex of the Northern Hemisphere”. Clearly, detailed biosystematic research is needed to resolve the problems in this group.

**Additional specimens examined**
Peru, Depto. Cuzco, peak between Machu Picchu ruins and Waina Picchu, 2400 m, 20 January 1976, L.E. Bishop 2504 (UC). Bolivia, Depto. Cochabamba, Prov. Chapare, road to San Onofre, 3–5 km N of road between Cochabamba and Villa Tunari, 1605 m, 29 October 1979, M.S. Foster 79–129 (UC); Prov. Ayopaya, Comunidad Pampa Grande, antes de llegar al primer rio que atravieza la senda desde Tunki, 16°40′S 66°28′W, 2030 m, 9 November 2002, Jimenez 1533 (LPB, UC); same locality, 2780 m, 18 September 2002, Jimenez 1667 (LPB, UC); Prov. Chachapata, Territorio Indigena Parque Nacional Isiboro-Secure, cordillera de Mose tenes, cresta arriba de laguna Carachupa, 16°14′S 66°25′W, 1550 m, 9 February 2003, Kessler 13146 (LPB, UC); Prov. Chapare, San Onofre, 1700 m, 27 February 1929, J. Steinbach 9401 (NY); Depto. La Paz, Prov. Nor Yungas, Estacion Biologica de Tunquin, Hornuni Bajo, senda cafetal al camino de la mina, 16°12′S 67°53′W, 2100 m, 29 August 2001, Bach 1711 (LPB, UC); same locality, 2000 m, 8 October 2002, Beck.
28374 (LPB), 2200 m, 16 August 2000, Jimenez 454 (LPB, UC), 2050 m, 18 November 2000, Krömer 1655 in part (GOET, LPB, UC); Prov. Sud Yungas, valle de Zongo, Santa Rosa, 16°07′S 68°05′W, 2390 m, 4 October 1998, de Boer 1119 (UC); Prov. F. Tamayo, PN-Anni Madidi, sendero Keara-Mojos, a 1 hora y media aproximadamente de caminata desde Tokuace por la senda al inciensal, 14°36′S 68°57′W, 2490 m, 11 March 2001, Jimenez 757 (LPB, UC); Prov. F. Tamayo, PN-Anni Madidi, senda Keara-Mojos, abajo de Tokuace, antes de la primera quebrada, 14°37′S 68°57′W, 2350 m, 11 October 2001, Jimenez 1001 (LPB, UC); Prov. F. Tamayo, Santa Ana, 14°55′S 68°23′W, 1700 m, 29 July 1902, Williams 1135 (NY); Prov. Abel Iturralde, PN-Anni Madidi, campamento de guardaparques Sadiri, camino Sadiri-Tumupasa, por la senda a las antenas de Entel, 14°10′S 67°53′W, 990 m, 7 July 2004, Jimenez 2649 (LPB, UC).

*Ceradenia setosa* M. Kessler & A.R. Sm., spec. nov.

(Fig. 3A–C)

**Etymology**

The name refers to abundant setae on this species, especially on the petiolo, abaxial laminar surfaces, and in sori.

**Type**

Bolivia, Dept. La Paz, Prov. Nor Yungas, Parque Nacional Biológica Cotapata, caminos alrededor de la Estación Biológica de Tunquini, 16°11′S, 67°52′W, 2300 m, 26 July 2000, Krömer 1370. Holotype: LPB.

**Diagnosis and description**

A species *Ceradenia tunquiniensis* differt statura majora, petioli brunneis, squamis rhizomatis longioribus, setis in superficie, pinnae sub angulo 80–90° a rhachidi patentes, setis in facie abaxiali laminae et setis brevibus albidis in sori.

Plants epiphytic; rhizomes stout, with dark orange-brown, slightly revolute rhizome scales to 5 × 0.8 mm, these with abundant pale marginal and superficial setulae; petiolo brown, to 170 × 1.8 mm, with abundant reddish setae to 1.8 mm, especially proximally, ca. 0.6–0.7 times as long as the lamina; rachis on both sides with sclerenchyma exposed, with reddish setae to 1 mm; laminae lanceolate, broadest in the lower third of the laminae, with one to six reduced proximal pinna pairs, apices not seen, pinnatisect, to 27 + cm long; pinnae to 40 × 7 mm, entire or very slightly repand, inserted 80–90° to rachises, at base widened to both sides, apices acuminate, abaxial costae, laminar surfaces, and margins with reddish setae to 1 mm, adaxial surfaces glabrous or with a few reduced setae to 0.2 mm, texture chartaceous; sori inframedial, to 11 pairs per pinna, superficial, with numerous whitish setae to

**Fig. 3.** *Ceradenia setosa* spec. nov.: (A) habit, (B) leaf detail, (C) rhizome scale (*Krömer 1370*). *Ceradenia tunquiniensis* spec. nov.: (D) habit, (E) leaf detail, (F) rhizome scale (*Krömer 1386*). All habit, leaf detail, and rhizome scale drawings are to the same scale, respectively.
0.7 mm, sporangia mixed with numerous, stalked, gland-tipped paraphyses.

Distribution and ecology
Endemic to Bolivia. *Ceradenia setosa* is a rare pendent epiphyte in humid montane forest at 2300 m (T. Krömer pers. comm.). Only a single individual was encountered during several months of intensive studies of epiphytic plants at the type locality.

Remarks
This is one of two Bolivian *Ceradenia* species with setose sori. It differs from *C. tunquiniensis* by its larger size, brown petioles, longer rhizome scales with superficial setae, pinnae inserted about 80–90° to rachises, setae on the abaxial lamina surfaces, and shorter, whitish setae in the sori. It is striking that these two quite similar but distinct species have both been found in the vicinity of the Estación Biológica de Tunquini.

*Ceradenia similis* M. Kessler & A.R. Sm., spec. nov.
(Fig. 2H–J)

Etymology
The name alludes to the similarity to related species of *Ceradenia*.

Type
Bolivia, Depto. La Paz, Prov. Nor Yungas, Parque Nacional Cotapata, Hornuní Bajo, senda del campamento Don Pedro hacia la mina, 16°12'S, 67°53'W, 2050 m, 18 November 2000, Krömer 1655 in part. Holotype, isotypes: GOET, LPB.

Diagnosis and description
Species nova *Ceradeniae* subg. *Filicipectenis* notis sequentibus: Setae abundae in lamina abaxiali, squamae rhizomatis castaneis, setulis marginalibus 0.2–0.5 plo quam latitudo squamae, pinnae angustae, sub angulo 60–80° a rhachidi patentes, distantes.

Plants epiphytic; rhizomes stout, with castaneous rhizome scales 3–0.3 mm, these with hyaline marginal setulae 0.2–0.5 times as long as the scale width; petioles dark brown to atropurpureous, to 19 cm × 1 mm, with scattered pale castaneous setae to 2 mm; rachis sclerenchyma adaxially exposed, dark brown, rachises abaxially greenish, both sides with abundant castaneous setae 0.3–0.5 mm; laminae lanceolate, with proximal pinna pair usually the largest, apices gradually reduced without a distinct apical segment, pinnatisect, basally sometimes fully pinnate, to 20 cm long; pinnae to 40 × 3 mm, slightly repand, separated by about their width, inserted 60–80° to rachises, widened and decurrent at base, especially basiscopically, apices acute to rounded, with numerous dark castaneous 0.3–0.5 mm setae on the abaxial lamina surfaces and costae, margins with regularly spaced blackish setae to 1 mm, adaxially with few scattered setae on the costae, texture thick-chartaceous; sori supramedial, to 15 pairs per pinna, superficial, lacking setae, sporangia mixed with numerous, stalked, gland-tipped paraphyses.

Distribution and ecology
Endemic to Bolivia. Known only from the type collection made at 2050 m in humid montane forest.

Remarks
This species is very similar to *C. pilipecten*, and indeed the type collection represents a mixed gathering of both species. *C. similis* is distinct in having darker rhizome scales with shorter marginal setulae, and narrower, more widely spaced, and more strongly ascending pinnae.

*Ceradenia tunquiniensis* M. Kessler & A.R. Sm., spec. nov.
(Fig. 3D–F)

Etymology
We name this species for the Biological Station Tunquini in Cotapata National Park, where intensive pteridological research has been carried out in the last few years and where this new species was collected.

Type
Bolivia, Depto. La Paz, Prov. Nor Yungas, Parque Nacional Cotapata, caminos alrededor de la Estación Biológica de Tunquini, 16°11'S, 67°52'W, 1550 m, 28 July 2000, Krömer 1386. Holotype: UC, isotype: LPB.

Diagnosis and description
Inter species paucas subg. *Filicipectenis* soris setosis notatas differt a *Ceradenia meridense* (Klotzsch) L.E. Bishop pinnis leviter ascendentibus (non fere perpendicularius et pinnis proximis saepe parum deflexis), textura laminae tenuior, squamis rhizomatis brevioribus et latioribus.

Plants epiphytic; rhizomes stout, with golden-brown to dark orange-brown rhizome scales to 3 × 0.4 mm, these with pale marginal setulae; petioles atropurpureous, to 90 × 0.8 mm, with castaneous setae to 2 mm, especially proximally, 0.6–0.7 times as long as the lamina; rachises on both sides with sclerenchyma covered by greenish tissue, with scattered castaneous setae to 1 mm; laminae lanceolate, broadest at or just above the base (lowermost zero to two pinna pairs slightly reduced), apices gradually reduced with a distinct elongate apical segment, pinnatisect, to 13 cm long; pinnae to 20 × 3.5 mm, entire or very slightly
repand, inserted 60–80° on rachises, at base widened and slightly decurrent, especially basiscopically, apices acute to rounded, costae and margins with castaneous setae to 1.5 mm, surfaces glabrous or with a few, scattered setae, texture chartaceous; sori medial to inframedial, to four pairs per pinna, superficial, with numerous castaneous setae to 1 mm, sporangia mixed with numerous, stalked, gland-tipped paraphyses.

**Distribution and ecology**

Endemic to Bolivia. A rare pendent epiphyte in humid montane forests at 1550 m (T. Krömer pers. comm.).

**Remarks**

This is one of two known Bolivian species in subg. Filicipecten with setose sori. It is most similar to north-Andean Ceradenia meridensis (Klotzsch) L.E. Bishop, which also has setose sori, but differs by the markedly ascending pinnae (vs. pinnae departing at roughly 90° from the rachises, with the proximal pinnae often somewhat reflexed), thinner blade texture, and shorter, broader rhizome scales. It differs from C. setosa, the only other Bolivian species with setose sori, by its shining atropurpureous petioles, shorter rhizome scales with only marginal setae, more ascending pinnae, glabrous or nearly glabrous laminar surfaces abaxially, and longer, castaneous setae in the sori. C. tunquiniensis is known only from the type collection which appears to be somewhat juvenile, even if it is fertile. It is thus conceivable that fully developed specimens could be significantly larger than indicated in the description.

**Key to the Bolivian species of Ceradenia**

1. Petioles lacking or shorter than 1/4 of blade length; rhizomes radially symmetric; whitish glands present on blade surfaces (subg. Ceradenia) ................................................................. 2
   – Petioles 1/4–3 times blade length; rhizomes dorsiventral; glands usually absent on blade surfaces (subgen. Filicipecten) ................................................................................................. 8
2. Blades simple, entire; rhizomes lacking scales ...................................................................... C. jungermannioides (Klotzsch) L.E. Bishop
   – Blades pinnatifid or more divided; rhizomes with scales ........................................................................ 3
3. Blades deeply pinnatifid ........................................................................................................ 4
   – Blades fully pinnate with well-spaced pinnae. ........................................................................... 6
4. Blades chartaceous, up to 11 cm long; rhizome scales 1–1.8 mm long, with gland-tipped marginal hairs; hydathodes present or absent ........................................................................................................... C. kalawayae M. Kessler & A.R. Sm.
   – Blades thick, fleshy, up to 45 cm long; rhizome scales 3–6 mm long, entire or setose; hydathodes absent .......................... 5
5. Pinnae 1–2 times as long as wide .................................................................................. C. discolor (Hook.) L.E. Bishop
   – Pinnae 3–7 times as long as wide .......................................................................................... C. pearcei (Baker) L.E. Bishop
6. Pinnae with setae 1–3 mm long; pinna margins sinuate. ........................................................ C. comosa L.E. Bishop
   – Petioles glabrous or with small, glandular hairs 0.1–0.3 mm long; pinnae entire to slightly sinuate or pinnatifid ......................................................................................................................... 6
7. Median pinnae up to 3(4.5) times longer than wide ......................................................... C. mirabilis L.E. Bishop
   – Median pinnae over 5 times longer than wide ................................................................... 9
8. Pinnae strongly ascending, inserted ca. 60° to rachises; setae pale castaneous. ........................................................................ C. ayopayana M. Kessler & A.R. Sm.
   – Pinnae slightly ascending, inserted ca. 80° to rachises; setae dark castaneous. ........................................................................ C. madidiensis M. Kessler & A.R. Sm. 10
9. Rhizomes long-creeping, petioles at least about 5 mm apart ........................................ C. bishopii (Stolze) A.R. Sm.
   – Rhizomes short-creeping, petioles < 2 mm apart ........................................................................ 11
10. Pinnae crenate ................................................................................................................. 12
    – Pinnae entire ..................................................................................................................... 13
11. Pinnae in 8–20 pairs, up to 6 cm long, thick-chartaceous . . C. clavipila L.E. Bishop ex M. Kessler & A.R. Sm.
    – Pinnae in 20–50 pairs, up to 2.5 cm long, thin-herbaceous . . . . . . C. madidiensis M. Kessler & A.R. Sm.
13. Pinna margins glabrous or with branched hairs up to 0.1 mm in length, rarely with a few setae..........................14
   - Pinnae at least with some marginal setae > 1 mm, lacking small, branched hairs.................................15
14. Rhizome scales orange-brown; rachises densely setose; costal sclerenchyma not visible........................15
   - Rhizome scales atropurpureous; rachises with pale hairs up to 0.1 mm in length and lacking setae; dark costal sclerenchyma exposed.................................................................C. glabra M. Kessler & A.R. Sm.
   - Rhizome scales atropurpureous; rachises with superficial and marginal setae; pinnae perpendicular to rachises; abaxial blade surfaces setose; setae in sori whitish, shorter than blade setae........................C. setosa M. Kessler & A.R. Sm.
15. Sori setose........................................................................................................................................16
   - Sori lacking setae...........................................................................................................................17
16. Petioles brown; rhizome scales up to 5.0 × 0.8 mm, with superficial and marginal setae; pinnae perpendicular to rachises; abaxial blade surfaces setose; setae in sori whitish, shorter than blade setae........................C. nudicarpa (Mart. ex Mett.) L.E. Bishop
   - Petioles atropurpureous; rhizome scales up to 2.0 × 0.6 mm, with marginal setae only; pinnae ascending, inserted 60–75° to rachises; abaxial blade surfaces glabrous; setae in sori brown, as long as blade setae.................................................................C. tunquiniensis M. Kessler & A.R. Sm.
17. Abaxial blade surfaces glabrous, with short brownish hairs or with a few scattered setae, especially on costae........................................................................................................................................18
   - Abaxial blade surfaces with abundant setae.....................................................................................19
18. Rhizome scales golden brown, 4.0–9.0 × 0.2–0.7 mm .................................................................C. spixiana (Mart. ex Mett.) L.E. Bishop
   - Rhizome scales castaneous, 2.5–8.0 × 0.2–0.4 mm ........................................................................19
19. Rhizome scales 5.0–8.0 × 0.2–0.4 mm ........................................................................C. clavipila L.E. Bishop ex M. Kessler & A.R. Sm.
   - Rhizome scales 2.5–3.5 × 0.2 mm ..................................................................................................C. nudicarpa (Copel.) L.E. Bishop
20. Rhizome scales dark castaneous, with setae along margins and on surfaces, especially towards scale bases......................................................................................................................C. pilipalea M. Kessler & A.R. Sm.
   - Rhizome scales golden brown to castaneous, with marginal setae only.............................................21
21. Rhizome scales golden brown, with some marginal setae > 1 times as long as scale width; blades abaxially glabrous, rarely with short brownish hairs or with scattered setae shorter than marginal setae..............................................................................................................C. spixiana (Mart. ex Mett.) L.E. Bishop
   - Rhizome scales orange-brown to castaneous, with marginal setae mostly shorter than scale width; blades abaxially with abundant setae about as long as marginal setae.................................................................C. similis M. Kessler & A.R. Sm.
22. Rhizome scales golden brown, with marginal setae 0.5–1.0 times as long as scale width; pinnae perpendicular to rachises, separated by less than half their width .........................C. pilipecten L.E. Bishop ex M. Kessler & A.R. Sm.
   - Rhizome scales castaneous, with marginal setae 0.2–0.5 times as long as scale width; pinnae ascending, inserted 60–80° to rachises, separated by about their width.................................................................C. similis M. Kessler & A.R. Sm.

**Grammitis setosora** M. Kessler & A.R. Sm., spec. nov.
(Fig. 4A–C)

**Etymology**
Named for the distinctive hairy sori.

**Type**
Bolivia, Depto. La Paz, Prov. Nor Yungas, Cerro Hornuni, por el sendero que va de la mina al 2do refugio, 16°12'S, 67°53'W, 2980 m, 20 December 2000, Jimenez 593. Holotype: UC, isotype: LPB.

**Diagnosis and description**
Inter speciebus neotropicis generis *Grammitidis* singularis soris hirsutis, laminis pilis albidis vel pallide brunneis, 3–4-cellularibus provisis et venis distinctis, furcatis, interdum anastomosantibus.

Plants epiphytic; rhizomes erect, with clathrate, reddish brown scales 1.3–3 × 0.3 mm, with two to three apical hairs 0.1–0.3 mm; petioles brown, 10–20 × 0.4–0.5 mm, with scattered whitish to light brown, 3–5-celled hairs to 0.3 mm, 0.15–0.3 times the length of the lamina; rachises abaxially with sclerenchyma exposed only in the proximal 1–2 cm of the laminae, on both sides with scattered, 3–4-celled, whitish to light brown hairs to 0.7 mm; laminae erect, thick-chartaceous, simple, linear-lanceolate, to 10 × 0.7 cm, apices rounded, on both sides with scattered, appressed, 2–5-celled, whitish to light brown hairs to 0.4 mm, margin sclerotic, dark brown, 0.15–0.25 mm, with an apiculum 0.2 mm on each laminar apex; veins 2–3-forked, casually anastomosing, inserted 40–50° to rachises; sori inframedial, placed on the acrosopic branch of the forked veins, superficial, elongate when immature, rounded when mature, with moderately dense, 4–7-celled, whitish to light brown hairs to 0.7 mm, lacking paraphyses.

**Distribution and ecology**
Endemic to Bolivia. Known from a single collection at 2980 m in wet cloud forest in Cotapata National Park.
Remarks
This intriguing species is easily recognized by its hairy sori, 3–4-celled, whitish to pale brown hairs on the laminae, and evident, forked, casually anastomosing veins. It is most similar to *G. marginella* (Sw.) Sw., from Central America and the Caribbean, which also has forked sterile veins and a hairy laminar surfaces. However, that species differs from *G. setosora* by lacking hairs in the sori, by having darker brown lamina hairs, and by its obscure, non-anastomosing veins. *Grammitis setosora* is also similar to *G. leptopoda* (C.H. Wright in N.E. Brown) Copel., which has weak, hyaline, deciduous hairs only on the laminar margins and veins, and evident, forked, non-anastomosing veins.

*Lellingeria carrascoensis* M. Kessler & A.R. Sm., spec. nov.
(Fig. 4D–F)

Etymology
Named after Carrasco National Park, the area with the highest recorded fern richness in the Neotropics (Kessler et al. 1999, 2001a, b), on whose boundary this new species was found.

Type

Diagnosis and description
Differt a *L. apiculata* (Kunze ex Klotzsch) A.R. Sm. & R.C. Moran rhachidi adaxiali fere glabra, squamis rhizomatis fuscati sparse setosis.

Plants epiphytic; rhizomes stout, short-creeping to erect, with dark castaneous, clathrate rhizome scales 2.5 × 0.4–0.7 mm, these with concolorous marginal setulae; petioles brown, to 60 × 0.7 mm, with scattered simple or one-forked gland-tipped hairs 0.1 mm, distally with a few short setae, about one-third as long as the lamina; rachises on both sides with dark sclerenchyma exposed, abaxially with scattered pale brown hairs 0.1 mm and dark, appressed hairs 0.1 mm, adaxially with erect, reddish hairs to 0.4 mm; laminae erect, lanceolate, broadest near middle, pinnatisect, to 14 cm long, gradually tapering to base and to pinnate apex;
pinnae to 30 × 3 mm, entire to very slightly repand, inserted 60–80° to rachises, at base widened and decurrent, especially basiscopically, apices acute to narrowly rounded, lamina surfaces glabrous or abaxially with scattered, pale hairs 0.05 mm on the costae and dark, appressed, club-shaped hairs 0.1 mm on the lamina surfaces near the rachises, margins with scattered, 2–3-celled glandular hairs to 0.1 mm, hydathodes not visible, texture chartaceous; sori inframedial, to six pairs per pinna, superficial, with several castaneous setae to 1 mm.

**Distribution and ecology**

*Lellingeria carrascoensis* is known from a single collection from a steep, wet slope with bushy vegetation at 3100 m.

**Remarks**

This new species is most similar to *Lellingeria apiculata* (Kunze ex Klotzsch) A.R. Sm. & R.C. Moran from which it differs by the essentially glabrous rachises abaxially and darker, more sparsely setose rhizome scales. The leaves of the type collection are shorter and relatively broader than is typical of *L. apiculata*, but whether this is characteristic of the species as a whole awaits further collections.

The type of *L. carrascoensis*, de Boer 1161, is a mixture of three species of superficially similar but not closely related grammitid ferns, also including *Ceradenia spixiana* and an undescribed species of *Terpsichore*.

*Lellingeria flagellipinnata* M. Kessler & A.R. Sm., spec. nov.

(Fig. 4G–I)

**Etymology**

Named for its distinctive, long-attenuate pinnae.

**Type**

Bolivia, Depto. La Paz, Prov. Nor Yungas, PN-ANMI Cotapata, trocha al valle de Coscapa, a 100 m de la carretera, 16°12'S, 67°53'W, 3400 m, 21 August 2002, Kessler 12901. Holotype: LPB; isotypes: AAU, GOET, NY, UC.

**Diagnosis and description**

Differt a *Lellingeria subsessilis* (Baker) A.R. Sm. & R.C. Moran statura majora (folia ad 35(65) cm longa vs. 15(20) cm), pinnae mediae longiores, longe attenuatae, petioli interdum 2–3(8) cm longi.

Plants epiphytic; rhizomes stout, short-creeping, with dark golden-brown to brown, clathrate rhizome scales 3–4.5 × 0.4–0.6 mm, these with pale marginal setulae and sometimes with a few occluded, dark cells on the scale base; petiolo atropurpureae, to 30(80) × 0.7(1) mm, with abundant pale brown, simple or basally 2–5-forked hairs 0.1–0.3 mm, 0.05–0.1 times as long as the lamina; rachises on both sides with dark selerenchyma exposed, with scattered, pale brown, simple or basally 2–3-forked hairs to 0.3 mm; laminae pendent, lanceolate, broadest near middle, pinnatisect, to 65 cm long, with numerous strongly reduced proximal pinnae, the lowermost often <1 mm, apices gradually reduced; pinnae to 120 × 3 mm, slightly repand, inserted 30–45° to rachises, at base widened and decurrent, especially basiscopically, apices often elongate, very long-attenuate, glabrous or with very few, scattered pale brown hairs to 0.2 mm on the costae, adaxially with well-marked hydathodes occasionally with calcareous secrerions, texture chartaceous; sori medial, often reaching beyond costa and margin when ripe, to 20 pairs per pinna, superficial, glabrous.

**Distribution and ecology**

Known only from Bolivia. *Lellingeria flagellipinnata* is a locally common species in cloud forests at (1700)2750–3500 m, where it co-occurs with *Terpsichore athyrioides* (Hooker) A.R. Sm., *T. laxa* (C. Presl) A.R. Sm., and several other, less common, pendent, epiphytic grammitids.

**Remarks**

The specimens placed in this species have long been identified as *L. subsessilis* (Baker) A.R. Sm. & R.C. Moran, widespread in the Neotropics. *Lellingeria flagellipinnata* differs by its larger size (well-developed leaves 25(30–35(65) cm long vs. 10–15(20) cm long) and much longer, narrower median pinnae that often have long, pendent, narrow apices. In *L. subsessilis*, the basalmost reduced pinnae are located just above the rhizome, while in *L. flagellipinnata* petioles are usually 2–3(8) cm long. The characteristic zigzag appearance of the laminae distally in *L. subsessilis* is only weakly discernable in *L. flagellipinnata*. In Bolivia, both species are well-separated elevationally, with *L. flagellipinnata* growing at (1700)2750–3500 m, while *L. subsessilis* occurs at 750–1500(2200) m, *Ceradenia comosa* L.E. Bishop is superficially quite similar to *L. flagellipinnata* but has glandular paraphyses and long, red setae on the stipes.

Specimens from Cochabamba tend to have somewhat shorter and slightly wider pinnae. The most divergent specimen, however, is *Buchtien 2753* (UC) from La Paz (Prov. Nor Yungas, Unduavi, 3300 m), which has conspicuously shorter, broader, and more closely spaced pinnae than is typical for *L. flagellipinnata*. Jimenez 580 has black fungal bodies emerging from the hydathodes.

Whether this species occurs outside Bolivia is uncertain. We have not seen specimens of *L. flagellipinnata* from elsewhere in the Andes, but a few
collections from Ecuador approach it in the elongate pinnae, e.g. Palacios 5520, MO, UC (Ecuador, Napo, Cantón El Chaco, Río Granadillo, Campamento de INECEL, “Codo Alto”, Bosque pluvial premontano, 00°08’S, 77°28’W, 1300 m). However, these Ecuadorian specimens differ from L. flagellipinnata in lacking petioles, having fewer pinnae, somewhat shorter leaves (intermediate between L. subsessilis and L. flagellipinnata), and in parallel-sided pinnae (vs. apically attenuate in L. flagellipinnata). We thus exclude these Ecuadorian specimens under L. flagellipinnata until this complex is better understood. Given its wide distribution in Bolivia, this species is expected to occur at least in southern Peru.

**Additional specimens examined**

Bolivia, Depto. Cochabamba, Prov. Chapare, Inca-chaca, 3300 m, 15 August 1950, Brooke 6731 (BM); Prov. Carrasco, arriba del primer sitio de camping del campamento Sehuenca, 17°31’S 65°16’W, 2400 m, 28 December 1999, Jimenez 181 (AAU, LPB, UC); Prov. Ayopaya, Comunidad Pampa Grande, sendero a Incacasi Grande, arriba del primer sitio de descanso, 16°40’S 66°28’W, 2560 m, 13 September 2002, Jimenez 1588 (LPB, UC); same locality, 2750 m, 18 September 2002, Jimenez 1669 (LPB, UC); Prov. Chapare, carrera nueva a Santa Cruz, pasando la represa de Coraní, 17°10’S 65°54’W, 3240 m, 29 September 2002, Jimenez 1742 (LPB); same locality, 3150 m, 29 September 2002, Jimenez 1749 (LPB, UC); Prov. Carrasco, Km 108 antiga carretera Cochabamba a Villa Tunari, 17°09’S 65°38’W, 2950 m, 22 June 1996, Kessler 6568 (LPB, UC); same general locality, Km 109, 2950 m, 23 June 1996, Kessler 6651a (LPB, UC), Km 104, 17°11’S 65°40’W, 3150 m, 25 June 1996, Kessler 6695 (LPB, UC), Km 100, 17°12’S 65°41’W, 3250 m, 26 June 1996, Kessler 6730 (LPB, NY, UC), Km 130, 17°07’S 65°36’S, 2000 m, 10 July 1996, Kessler 7178 (LPB, UC), Km 135, 17°06’S 65°34’W, 1700 m, 17 July 1996, Kessler 7366 (LPB, UC), Km 95–96, 17°13’S 65°42’W, 3400 m, 24 October 1999, Stähli 5155 (AAU); Prov. Carrasco, Km 8 Empalme a Siberia, 17°46’S 64°48’W, 2900 m, 22 October 1996, Kessler 9195 (LPB, UC); Prov. Carrasco, 28 km al noroeste de Comarapa por el camino entre Santa Cruz y Cochabamba, 17°49’S 64°41’W, 2450 m, 10 February 1987, Solomon 15987 (MO, NHA, NY, UC); Prov. Chapare, Llantas Aduana, 3100 m, 09 March 1929, J. Steinbach 9553 (BM); Prov. Carrasco, near pond along road from Cochabamba to Comarapa, 5.5 km E of El Churro, 17°50’S 64°44’W, 2975 m, 16 April 2002, Sundue 642 (LPB, NY, USZ); Depto. La Paz, Prov. Nor Yungas, Estación Biológica de Tunqui-ní, senda del campo de Don Pedro, al camino de la mina (Bajo Hornuni), 16°11’S 67°53’W, 2600 m, 09 December 2000, Bach 988 in part (LPB, UC); same general locality, 3000 m, 14 September 2000, Bach 1046 (LPB, UC), Bach 1051 (LPB), 16°12’S 67°53’W, 2575 m, 08 April 2001, Bach 1383 (LPB), 16°11’S 67°54’W, 3100 m, 08 August 2001, Bach 1455 (LPB), 3000 m, 07 December 2002, Bach 1807 (LPB), 13 July 2002, Bach 1822 (LPB), 2800 m, 16 July 2002, Bach 1878 (LPB, UC) 2980 m, 20 December 2000, Jimenez 44 (LPB, NY), 2450 m, 14 August 2000, Jimenez 438 (LPB, NY); Prov. Nor Yungas, Chusipata 2 km hacia el S via antiguo tramo ferroviario, 3000 m, 24 July 1988, Beck 13850 (LPB, NY); Prov. Nor Yungas, pasando Unduavi antes de llegar a Cotapata, subiendo la senda antigua hacia Coroico, 3500 m, Beck 21491 (LPB, UC); Prov. Nor Yungas, Unduavi, 3300 m, November 1910, Buchten 2753 (UC); Prov. Nor Yungas, Chusipata, 3000 m, 17 August 1957, Cañigueral 855 (LPB); Prov. Nor Yungas, Cotapata, roadsside behind gas station, 16°15’S 67°50’W, 3225 m, 27 July 1989, Fay & Fay 2454 (LPB, MO); Prov. Sud Yungas, Cotapata, north on trail on side of mountain, 16°15’S 67°50’W, 3200 m, 08 August 1989, Fay & Fay 2613 (LPB, MO, UC); Prov. Sud Yungas, Unduavi, cerca a la Mina Lourdes, 16°18’S 67°52’W, 3450 m, 25 November 1995, Gonzales 1567 (LPB), Gonzales 1571 (LPB); Prov. Nor Yungas, Coscapa, sobre el sendero prehispánico Sillutinkara, 16°12’S 67°53’W, 3480 m, 16 January 2001, Jimenez 580 (LPB); same locality, 3450 m, 09 September 1997, Kessler 11173 (LPB, UC), 3000 m, 12 September 1997, Kessler 11867 (LPB, UC), 16°17’S 67°54’W, 3450 m, 30 April 1988, Lewis 88338 (MO, UC), 16°17’S 67°53’W, 3400 m, 05 May 1990, Luteyn 13482 (LPB, NY, UC), 3500 m, 16 September 1997, J. Müller 6136 (LPB, NY); Prov. F. Tamayo, PN-ANMI Madidi, senda Keara-Mojos, abajo de Chunkani, 14°38’S 68°57’W, 2870 m, 11 August 2001, Jimenez 907 (LPB); same general locality, 14°41’S 68°58’W, 3470 m, 29 April 2003, Jimenez 1772 (LPB); Prov. B. Saavedra, Km 15 Charazani a Chullina, 15°10’S 68°53’S, 3400 m, 05 July 1997, Kessler 10629 (LPB, UC); Prov. Nor Yungas, Km 2 Chusipata a Coroico, 16°22’S 67°49’W, 2900 m, 17 September 1997, Kessler 11910 (LPB, UC); same general locality, 16°23’S 67°48’W, 2750 m, 18 September 1997, Kessler 12024 (LPB, UC); Prov. Nor Yungas, 1 km W of Chusipata, 16°17’S 67°49’W, 3140 m, 24 March 1982, Solomon 7261 (MO, UC); same general locality, 16°17’S 67°50’S, 3100 m, 26 June 1986, Solomon 15339 (MO, NHA, UC), 16°18’S 67°49’W, 3100 m, 21 January 1988, Solomon 17593 (LPB, NY), 16°19’S 67°50’W, 3000 m, 28 July 1980, Windsch 2440 (LPB); Prov. Sud Yungas, 1.4 km W of Unduavi, on new road between Chusipata and La Paz, 16°18’S 67°55’W, 3400 m, 02 July 1986, Solomon 15402 (MO, NY); Depto. Santa Cruz, Prov. Caballero, entre Comarapa y Siberia, ca. 1 km de Siberia a Comarapa, 17°49’S 64°44’W, 2500 m, 18 March 2003, Lehnert 718 (UC); Prov. Caballero, por un pequeño lago hacia la cumbre pasar 4 km E de Siberia, 2800 m, 04 January 2000, Wood 15791 (LPB).
Key to the Bolivian species of *Lellingeria*

1. Blades <4(5) mm wide; proximal sterile blade portions serrate, apical fertile portions entire. .................................................. *L. myosuroides* (Sw.) A.R. Sm. & R.C. Moran
   - Blades >8 mm wide; not differentiated into sterile and fertile portions ............................................. 2
2. Fertile median pinnae <8(9) mm long .......................................................... *L. phlegmaria* (J. Sm.) A.R. Sm. & R.C. Moran var. *phlegmaria*
   - Fertile median pinnae > (8)10 mm long .................................................. 7
3. Pinnae acroscopically gibbous ............................................... *L. humilis* (Mett.) A.R. Sm. & R.C. Moran
   - Pinnae entire or nearly so .................................................. 4
4. Pinnae <1.5 times longer than wide .......................................................... *L. humilis* (Mett.) A.R. Sm. & R.C. Moran
   - Pinnae >2 times longer than wide ........................................................................ 5
5. Rhizome scales <0.5 mm long .......................................................... *L. sinacensis* (Rosenst.) A.R. Sm. & R.C. Moran
   - Rhizome scales >1.5 mm long ........................................................................ 6
6. Hairs on rachises brown, thick; epiphytic, mature plants often pendent .................................................. *L. suspensa* (L.) A.R. Sm. & R.C. Moran
   - Hairs on rachises white, thin; terrestrial and saxicolous, mature plants erect
      - Pinna bases slightly constricted, distant; rachises partly free on both sides
         - Sinuses between pinnae at most about as wide as pinna ............................................. 8
      - Sinuses between pinnae at least 1.5 times as wide as pinna ............................................. 11
   - Mature leaves >15 cm long ........................................................................ *L. major* (Copel.) A.R. Sm. & R.C. Moran
      - Mature leaves <10(15) cm long ........................................................................ 10
   - Rachises glabrous or nearly so; proximal pinnae triangular .................................................. *L. obovata* (Copel.) A.R. Sm. & R.C. Moran
      - Rachises densely hairy; proximal pinnae rudimentary .................................................. *L. tenuicula* (Fée) A.R. Sm. & R.C. Moran
   - Pinnae strongly ascending, inserted ca. 45° to rachises .................................................. 12
   - Pinnae slightly ascending, inserted ca. 60–80° to rachises .................................................. 13
   - Mature leaves (25)30–35(55) cm long; many pinnae elongate, with long, attenuate apical portions
      - Mature leaves 10–15(20) cm long; if a few elongate pinnae present, these not apically attenuate
         - Sori with setae up to 1 mm long; abaxial blade surfaces glabrous or with scattered dark, appressed hairs near rachises .................................................. *L. carrascoensis* M. Kessler & A.R. Sm.
      - Sori lacking setae; abaxial blade surfaces with tiny, brown, unbranched, appressed hairs
         - Rachises with dense hairs on both sides ........................................................................ *L. apiculata* (Kunze ex Klotzsch) A.R. Sm. & R.C. Moran
      - Rachises glabrescent at least on one side .................................................. 14
   - Rachises with dense hairs on both sides ........................................................................ *L. apiculata* (Kunze ex Klotzsch) A.R. Sm. & R.C. Moran
      - Rachises glabrescent at least on one side .................................................. 14

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